WOOD STRUCTURE IN RELATION TO GROWTH IN *EUCALYPTUS GIGANTEA* Hook. f.

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Summary

A survey has been made of the structure of the wood of *Eucalyptus gigantea* Hook. f. in relation to growing conditions in the Australian Capital Territory. Using the number of cells cut off by the cambium at various intervals during the growing season as a measure of growth, mathematical expressions have been obtained for growth in young trees at ground level, breast height, and half height; from these, growth rate curves have been derived. The time of year at which growth commences, the relationship of vessel production to commencement of growth, the formation of late wood, and the period of dormancy have all been considered in detail. Variations in fibre dimensions have been investigated in relation to growth and it has been shown that in any one growth ring the shortest fibres are found in the early wood and the longest in the late wood. An intrinsic relationship between growth rate and fibre dimensions has been established, and, at the junction between late and early wood, a sudden change in fibre dimensions occurs corresponding to the discontinuity in growth rates. Anomalous woody tissue formed during severe drought conditions is also described.

I. Introduction

Eucalyptus gigantea Hook. f. (syn. *E. delegatensis* R. T. Baker) occurs in relatively pure stands in the highlands of south-eastern Australia—in Victoria, south-eastern New South Wales, and the Australian Capital Territory at elevations of 3000-4500 ft., and in Tasmania between 1800 and 3000 ft. The size of the tree varies, but on favourable sites it may attain heights up to 300 ft. and stem diameters breast high up to 5 ft. The tree yields valuable timber which has a wide variety of commercial uses. The structure of the wood is of considerable interest in that it shows definite growth rings, a feature possessed by only a few other eucalypts, and also gives an impression of ring-porosity which, however, is quite unlike the well-known ring-porous timbers such as oak, ash, hickory, etc. Examination of cross sections cut from many specimens obtained from Victoria, New South Wales, and the Australian Capital Territory has revealed that the ring of pores observed macroscopically is confined more or less to the early wood and that, in addition, in many growth rings the first-formed early wood is devoid of pores. This is, of course, a distinctive difference from the typical ring-porous timbers in which there is always a ring of very large pores in the first-formed early wood. Another characteristic of the growth ring of *E. gigantea* is that there is, in most cases, a very distinctive band of late wood where again few, if any, pores occur. These two attributes

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are most marked in specimens from the mainland but are ill-defined in specimens grown in Tasmania. Comparative photomicrographs as shown in Plate 1 clearly illustrate this point.

It was considered that some information regarding this rather unusual wood structure might be obtained from the systematic examination of the wood laid down during the growing season. It was intended to determine whether, in this species of eucalypt, there is a definite cessation of growth, and when renewal of growth occurs after the formation of late wood. For the purpose young saplings from the Australian Capital Territory were used; these were obtained through the cooperation of the Commonwealth Forestry and Timber Bureau at regular intervals during a period of two years. A record of the wood laid down during the whole growing season and the relationship between growing conditions and types of tissue formed were obtained. In addition it was planned to investigate the variation, if any, in fibre dimensions with respect to growth rate during any one growing season.

There is some importance in determining growth relationships for this species since Moulds (1947) and Jolly (1948) have both drawn attention to the possibility of its use for exotic plantations and its successful employment for exotic reafforestation projects has been predicted by Martin (1948) provided that conditions of frost do not fall below 10°F.

II. Material

From January 1945 to October 1946, with the exception of May, June, and July 1946, three saplings per month were obtained by random selection from an even-aged (approximately 12 years old) regrowth stand of *E. gigantea* in the highlands of the Australian Capital Territory where the forest is of the sclerophyll woodland eucalypt type, the average rainfall 30 in., and the area subject to severe frosts from March to November. In this locality the mean annual temperature is 58°F., ranging from an average minimum of 30°F. in July to an average maximum of 80°F. in January, and the area is sometimes under snow during the winter months. Each sapling was approximately 12 ft. in height and, from each, cross-sectional discs were cut at ground level, breast height, and half height. These discs were used in all examinations. For comparison, specimens of *E. gigantea* from various localities within its range of occurrence were examined; these specimens were taken from the standard wood collection of the Division of Forest Products, C.S.I.R.O.

III. Experimental

Thin cross sections were cut from each disc, care being taken to include the last-formed woody tissue in each case, and these were used for the routine microscopic examinations. In addition to noting the general character of the developing growth rings an attempt was made to gauge the level of cambial activity for each period by counting the number of cells cut off in radial rows subsequent to the formation of the late wood of the previous growing season. Because the growth ring varies in width within the one tree, sections were taken from what was considered to be the average width of the growth ring and in many cases average counts from opposite sides of the tree were used.

For the work on fibre dimensions, one tree cut in March 1945 was specifically selected and the three discs taken at ground level, breast height, and half height used. From the discs, blocks extending from the pith to the outside of the stem and approximately ⅜ in. in width, were prepared. From each block a transverse section, 20 μ in thickness, was cut, stained, and mounted in the usual manner. These sections were used for general observation, fi
diameter measurements, and subsequent positioning of the tangential sections cut from the remainder of the blocks. Growth rings were numbered from the bark inwards to the pith 1-11 at ground level, 1-8 at breast height, and 1-5 at half height.

Serial longitudinal tangential sections 80 μ in thickness, were cut from each block, working from the bark side to the pith. From the cross sections referred to above the width of each growth ring was accurately measured and the position of the longitudinal tangential section precisely determined. These were cut approximately parallel to the growth rings, but as the pith was approached the curvature of the growth rings increased and, therefore, the width of the tangential section was progressively reduced in order to retain parallelism to the growth rings. Separation of each section into its component fibres was effected by treatment with equal parts of glacial acetic acid and 100 vol. hydrogen peroxide at 50°C. for 17 hours followed by a further treatment at 100°C. for 2 hours in the same mixture. The supernatant liquid was decanted and then a small quantity of water was added to the treated section. After gentle agitation the fibres readily separated. A suspension of the separated fibres was in each case transferred to a glass slide and fifty fibres chosen at random were measured. The average fibre length for each pre-selected position in the growth ring was thus obtained.

For the determination of radial fibre diameters throughout the growth ring the radial distances occupied by successive groups of five fibres were measured and averaged.

IV. Results and Discussion

(*a*) *Growth in Diameter at Various Levels*

The numbers of cells produced radially at the various levels during the growing season are set out in Table 1 and graphically illustrated in Figure 1. For each cell count a different tree was used, hence individual variations in growth rate are responsible for a marked scatter in the results, but because of the number of trees involved the analysis of the results gives a truer picture of growth than would have been the case had all samples been drawn from the one tree. The final values to which the curves in Figure 1 approach were obtained from the averages of cell counts made on 46 trees, using the 1943-44 and 1944-45 growth rings. The numbers of cells in these two growth rings were approximately the same and agreed with the later values recorded for the 1945-46 growth ring. The more apparent features of the growth curves obtained are summarized in Table 2.

For an approximate picture of diameter growth in the bole, and to represent its periodic nature, an equation was derived of the form:

$$y = a + bx + c \sin x + d \cos x + e \sin 2x + f \cos 2x,$$

where $y =$ the number of cells cut off by the cambium at any particular time during the growing period and $x = \frac{360}{365}$ times the number of days from January 1 (chosen as an arbitrary reference point, see Table 1), x therefore expresses the phase angle of the annual cycle and is measured in degrees. In fitting the equation to the three sets of data for ground level, breast height, and half height respectively, the last three terms did not significantly improve the fit and they were therefore omitted, giving an equation of the form:

$$y = a + bx + c \sin x.$$

TABLE 1

NUMBERS OF CELLS MATURED FROM CAMBIUM INITIALS AT VARIOUS TIMES DURING THE YEAR

Days	Days Converted to Degrees	Date	Number of Cells Ground Level	Number of Cells Breast Height	Number of Cells Half Height
16	16	16.i.45	103	126	138
33	33	2.ii.45	114	128	179
68	67	9.iii.45	119	130	178
94	93	4.iv.45	167	200	268
121	119	1.v.45	206	217	272
169	167	18.vi.45	153	199	190
196	193	vii.45	113	122	162
227	224	viii.45	193	220	279
258	254	ix.45	203	214	227
285	281	12.x.45	13	23	19
333	328	29.xi.45	71	55	62
353	348	19.xii.45	96	108	108
18	18	18.i.46	136	148	131
53	52	22.ii.46	118	121	135
81	80	22.iii.46	118	162	163
114	112	24.iv.46	184	235	251
205	202	24.vii.46	225	275	275
234	231	22.viii.46	170	173	216
260	256	17.ix.46	171	3	6
284	280	11.x.46	11	20	22

The fact that the term in cos x is not significant has the interpretation that the date of maximum growth rate does not differ significantly from January 1, nor the date of minimum growth rate from July 1. The fitted curves of the form $y = a + bx + c \sin x$ are not satisfactory since in two cases they show a decrease about the time of minimum growth rate, which is physically impossible. Adjusted curves were therefore fitted with the restriction that the minimum value of the growth rate should be zero (i.e. $dy/dx = 0$, when $d^2y/dx^2 = 0$). As $dy/dx = b + c\pi/180 \cos x$ and $d^2y/dx^2 = - c\pi^2/180^2 \sin x$, minimum growth occurs when $\sin x = 0$, i.e. $x = 180°$ (corresponding to July 1) and $b = c\pi/180$.

The equations for the fitted curves then become:

$$\begin{aligned}
&\text{Ground level} & y &= 86.4 + 0.503\,x + 28.3\,\sin x,\\
&\text{Breast height} & y &= 99.5 + 0.569\,x + 32.6\,\sin x,\\
&\text{Half height} & y &= 112 + 0.668\,x + 38.3\,\sin x.
\end{aligned}$$

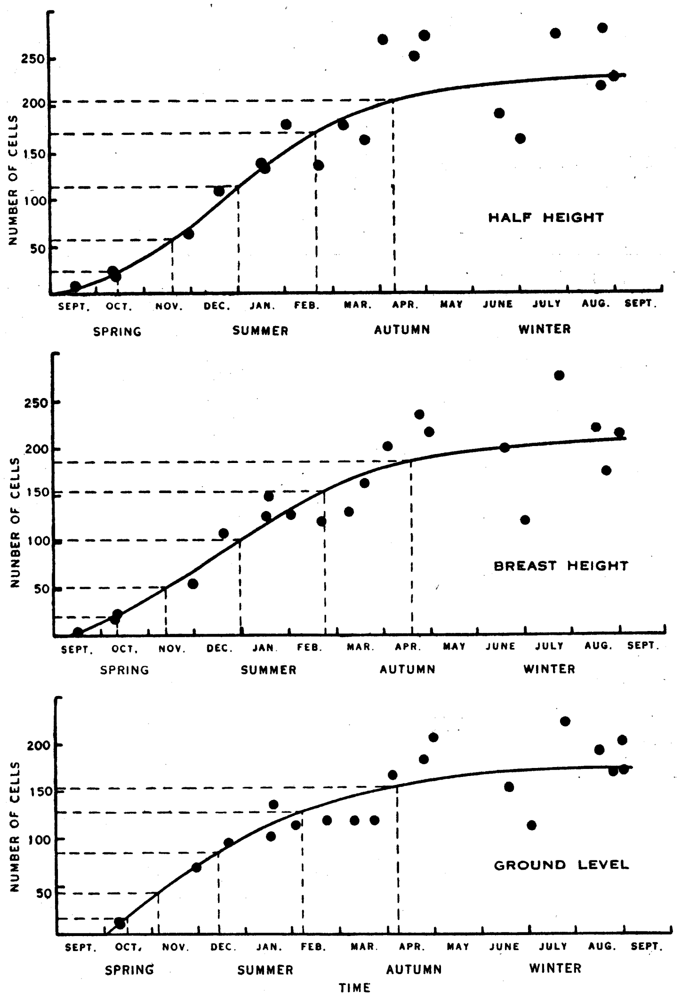

Fig. 1.—Summation curve of growth as determined by cell counts. At half height (upper), breast height (middle), and ground level.

These curves and the derived growth rate curves are shown graphically in Figure 2. From the above equation it is deduced that the new growth ring commences about September 1 and that the period May 1 to September 1, two months on either side of the date of minimum growth rate, may be regarded as a period of little or no growth. From Figure 1 it is apparent that less than one-tenth of the growth ring is added over this period.

Mathematical expressions of this type are, of course, merely broad generalizations. The very nature of their derivation implies a continuity of improvement and deterioration in growth condition whereby the growth rate increases steadily to a maximum and falls steadily to zero. This occurs relatively rarely, if ever, in nature. The adjustments involved produce inaccuracies which become magnified in the derived curves (as will become apparent later) but the expressions do give a working approximation to the amount of growth which can be expected in the species growing on the site under examination.

TABLE 2

SUMMARY OF MORE OBVIOUS FEATURES OF THE GROWTH CURVES OF *E. GIGANTEA* AT DIFFERENT LEVELS

Characteristic	Ground Level	Breast Height	Half Height
Growth commences	Last week in September to first week in October	Second week in September	Early September
First tenth of ring completed	Mid October	Second week in October	Mid October
First quarter of ring completed	Early November	Second week in November	Third week in November
Half ring completed	Mid December	End of December	First week in January
Three-quarters of ring completed	Early February	Late February	Late February
Nine-tenths of ring completed	Early April	Mid April	Mid April
Average number of cells cut off in one year	171	205	227

(*b*) *Commencement of Growth*

Working with timber species of the northern hemisphere Priestley, Scott, and Malins (1933) noted that resurgence of cambial activity took place first in the crown behind the growing shoots and progressed with variable rapidity, depending on species, down the trunk. In some species the progress of the growth stimulus was very rapid and in others much more protracted. The growth curves in Figure 1 suggest that *E. gigantea* is of the latter type, growth at ground level beginning about three weeks later than at half height. In order to confirm these observations some sample trees were felled every three or four days during the last month (Sept.-Oct. 1946) of the experiment. The first indication of cambial activity for the new growing season was observed on September 6, September 13, and October 1 for half height, breast height, and ground level respectively. The same conclusion may also be drawn from a

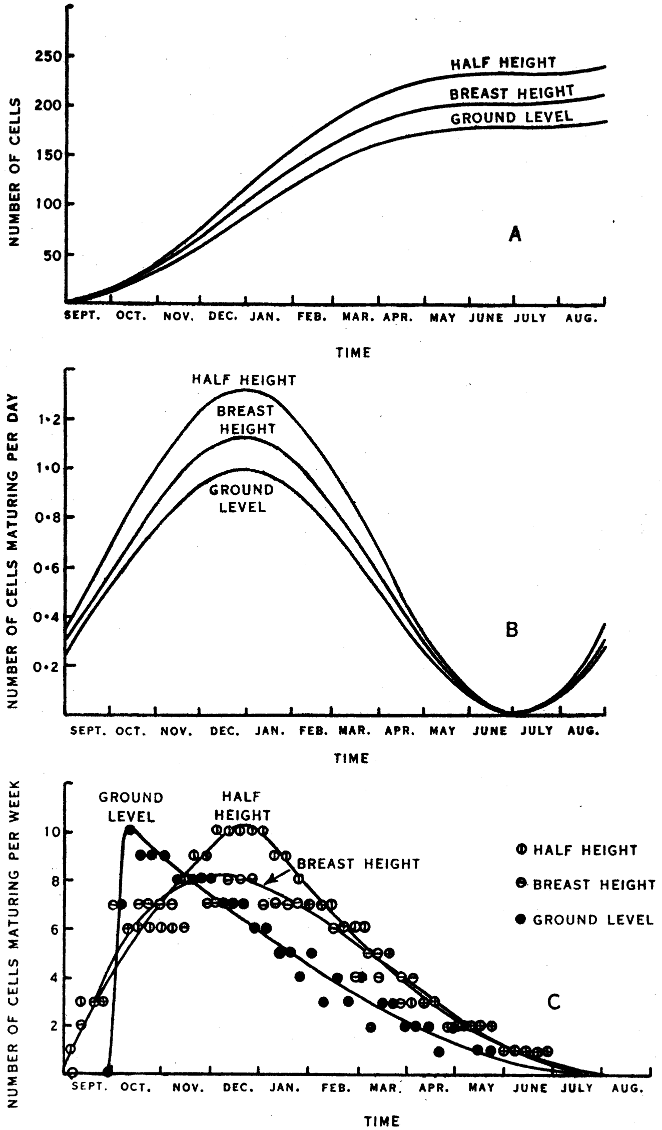

Fig. 2.—Fitted growth curves and growth rate curves, both derived and actual.

(*A*) Fitted growth curves for the three levels, half height, breast height, and ground level.

Half height $y = 86.4 + 0.503\ x + 28.3 \sin x$,
Breast height $y = 99.5 + 0.569\ x + 32.6 \sin x$,
Ground level $y = 112 + 0.668\ x + 38.3 \sin x$

$(x = \frac{360}{365} \times \text{no. of days from Jan. 1})$.

(*B*) Derived growth rate curves $dy/dx = b + c\pi/180 \cos x$.

(*C*) Growth rates at various levels determined as a curve of increments.

study of the 1944-45 growth ring in the various trees collected for examination. Specimens from half height invariably showed two bands of abnormal tissue (Plate 2, Figs. 1-3); some specimens from breast height showed two bands and others only one; specimens from ground level showed one band only (Plate 2, Fig. 4) and that not always well developed. The two bands at half height were always about 20 cells apart and one always appeared at the commencement of the growth zone, sometimes after a few fibres had been produced. As the two bands occurred in all trees from the stand it can be accepted that the same causal agent was responsible and therefore conditions conducive to the production of abnormal tissue arose twice during the early period of growth in September and October 1944. One band did not always appear at breast height, indicating that the cambium was still dormant at this level in some trees when this band of abnormal tissue was being produced at half height. At ground level, where only one band (the second in the growth period) appeared, it was always at the beginning of the growth ring, indicating a definite time lag between commencement of growth at half height and ground level sufficient for the production of 20-25 cells at half height.

Initiation of growth is dependent upon the interaction of a number of internal and environmental factors, of which the descent of hormone and nutrients from the crown, the insulating effect of the ground, and photoperiodic factors probably have separate influences. Consideration of such interactions is beyond the scope of this paper but it has been established that it takes a period of 3-4 weeks for conditions suitable for cambial division to progress a distance of some 6-7 ft. down the bole, at least in young saplings.

(*c*) *Woody Tissue laid down during Early Stages of Growth*

The examination of the material collected from the Australian Capital Territory shows that, upon resumption of cambial activity in the spring, a number of fibres readily distinguishable from the late wood of the previous growth ring are produced (see Plate 1, Fig. 1). Vessels are infrequent, usually entirely absent, in these first-formed cells. The same feature has been observed in numerous specimens of this species from New South Wales, Victoria, and the Australian Capital Territory (see Plate 1, Fig. 4) but not in specimens from Tasmania, which show an obviously different arrangement, the late wood of each growth cycle being poorly defined (Plate 1, Fig. 2). The difference is well illustrated in Figure 3 in which a comparison has been made between the number of fibres produced by the cambium before the first formation of vessels in specimens from the Australian Capital Territory and a number of Tasmanian trees. The data have been summarized in Table 3. From the table and the histograms it appears that the Tasmanian trees belong to a different statistical population from those of the Australian Capital Territory. Not all mainland specimens of *E. gigantea* fall into the latter class; occasionally intermediate types are noted, but the great majority follow the pattern observed for the Australian Capital Territory specimens. From the histograms in Figure 3 it is evident that initial vessel formation in the Australian Capital Territory specimens is most rapid after some 18-20 fibres have been developed by the cambium, the time of this maximum vessel formation corresponding to about mid October. This is subsequent to the development of approximately one-tenth of the growth ring.

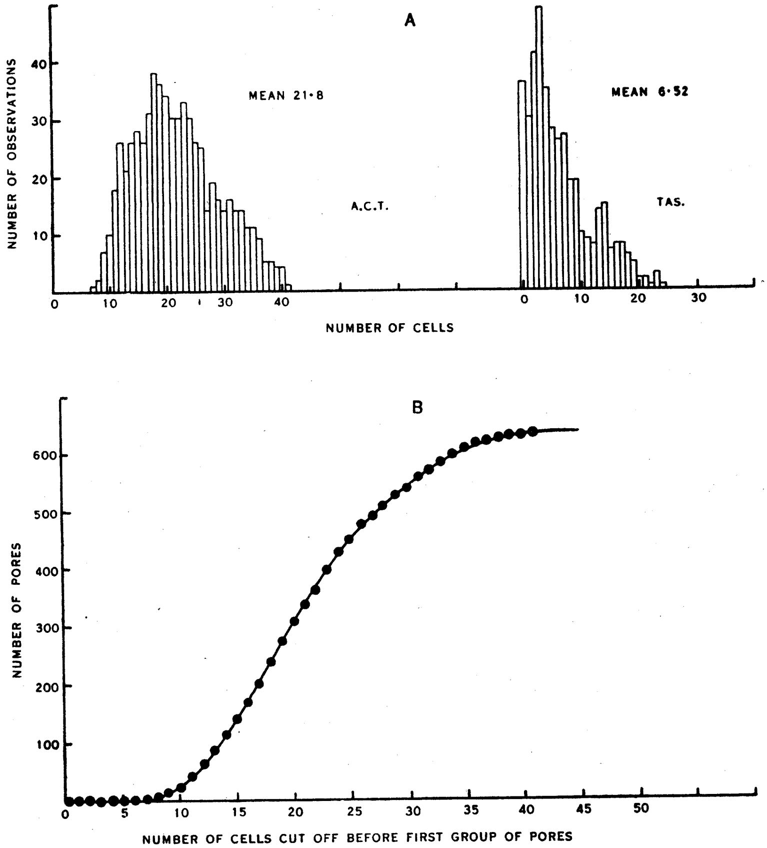

Fig. 3.—Number of fibres cut off by cambial initial before production of first vessel.

(*A*) Histograms of Australian Capital Territory and Tasmanian samples compared.

(*B*) Cumulative curve of Australian Capital Territory histogram in Figure 2 (*A*).

The delay in vessel formation at the commencement of growth is, of course, quite distinct from what is observed in northern hemisphere species where the flush of growth in spring is accompanied by the immediate formation of vessels, which, in the typical ring-porous species, are very large in comparison with those formed later in the season. It is of interest to note, however, that in one sample of *Fagus sylvatica* L. examined in this laboratory there was definite evidence of the development of up to five rows of fibres in the first-formed early wood before the development of vessels.

The fact that the vessel pattern in *E. gigantea* differs according to the origin of the specimen, namely whether from Tasmania or the mainland, suggests that climatic and environmental factors are responsible for appreciable variations in anatomical structure. However, the possibility of an inherent varietal difference has not been overlooked, and seed of Australian Capital Territory origin is being grown in Tasmania and vice versa. Examination of the wood structure of the two groups will be made when they reach the sapling stage.

TABLE 3

OCCURRENCE OF FIRST-FORMED VESSELS IN THE EARLY WOOD OF *E. GIGANTEA*

Range (Number of Fibres before First Vessel)	Percentage of First Vessels in Range	
	A.C.T. Material	Tasmanian Material
0- 9	1.6	75.7
10-19	41.3	22.1
20-29	40.0	2.2
30 and over	17.1	Nil

A further observation on the vessel pattern from pith to bark of 15 Australian Capital Territory specimens selected at random suggests a relationship between distance from the crown and number of fibres produced before vessel development. In each growth ring at ground level the average number of fibres produced before the first formation of vessels was determined; the results are summarized in Table 4. It is apparent that the number of fibres maturing before vessels are produced increased with age of the tree. This is also apparent at higher levels and it was observed that in any one growth ring the number of fibres cut off by the cambium before vessel formation decreased from ground level up to half height. It is possible therefore that the crown of the tree is intimately connected with vessel production.

It is fairly generally accepted that resurgence of cambial activity in the stem is associated with the descent of hormone from the crown. From the above evidence it would also appear that the time of vessel production in relation to commencement of growth is also dependent on distance from the crown. Cambial activity, in the trees examined, was initiated at ground level 3-4 weeks later than at half height; delay in vessel production over the same distance may be as much as 6-8 weeks. This phenomenon could be explained on the basis of the supposition that the crown produced two substances, one initiating cambial division and the other stimulating vessel production, the latter descending from the crown at a slower rate than the former. The bands of vessel-free (or comparatively so) late wood in mainland specimens of *E. gigantea* would result from the inactivation of one of these stimuli and cessation of growth from the inactivation of the other. Late production of vessels in those portions of the woody stem removed from the crown would be repeated in each growth cycle. It is possible that the stimulus affecting vessel production is more sensitive to climatic and environmental changes than the growth stimulus. In those trees, particularly from Tasmania, where it is assumed that growth does not entirely cease, as evidenced by indistinct growth rings, there would not be complete inactivation of either stimulus, and both growth and vessel development would be continuous.

TABLE 4

NUMBER OF FIBRES PRODUCED IN GROWTH RINGS OF *E. GIGANTEA* FROM THE AUSTRALIAN CAPITAL TERRITORY AT GROUND LEVEL BEFORE FIRST VESSELS

Ring	Range	Average
1934-35	0	0
1935-36	0–1	0
1936-37	0–4	1
1937-38	1–10	3
1938-39	1–16	4
1939-40	3–11	5
1940-41	3–11	5
1941-42	4–16	9
1942-43	6–24	13
1943-44	6–27	14
1944-45	9–42	21
1945-46	11–43	22

(*d*) *Variation in Growth Rate*

Growth rates have been expressed throughout the growing season as curves derived from the equations of the form $y = a + bx + c \sin x$ fitted to the cell count data (see Fig. 2*B*) and also as curves of increments from the actual growth curves (see Fig. 2*C*). As noted earlier, many of the small differences between growth at the different levels and the more subtle growth characters that are intimately related to the structure of the wood are masked by the mathematical treatment. Substituting the known values of b and c in the equation $dy/dx = b + c\pi/180 \cos x$, maximum growth rates on January 1 may be calculated. These are 0.99, 1.12, and 1.32 cells per day for ground level, breast height, and half height respectively.

The curves of increments, however, show variations in the dates of maximum growth rates although their magnitudes are not appreciably different from the calculated values. Growth begins at ground level 3-4 weeks later than at half height but the maximum growth rate of about 10 cells per week is reached within a fortnight and thereafter falls off slowly over the remainder of the growing season. On the other hand, the growth at half height increases more slowly, taking about four months to reach a maximum, also of about 10 cells per week, at which time the growth rate at ground level has been reduced to $^3/_5$ of its maximum. From midsummer onwards the growth rate at all levels falls off over the remainder of the growth period, reaching zero in late winter. In general the resurgence of cambial activity occurs sooner nearer the crown but the achievement of maximum growth rate is most rapid near the bottom of the stem.

(*e*) *Late Wood Formation and Dormancy*

The first sign of late wood formation in the Australian Capital Territory specimens, i.e. thickening of the cell wall followed by a reduction in the radial diameter of the cell, takes place towards the end of May or beginning of June since the trees felled in mid June showed a little late wood formation.

One of the original purposes of this study was to determine whether or not *E. gigantea* growing in the Australian Capital Territory passes through a dormant stage, and, if so, to estimate the length of this period. In late August,

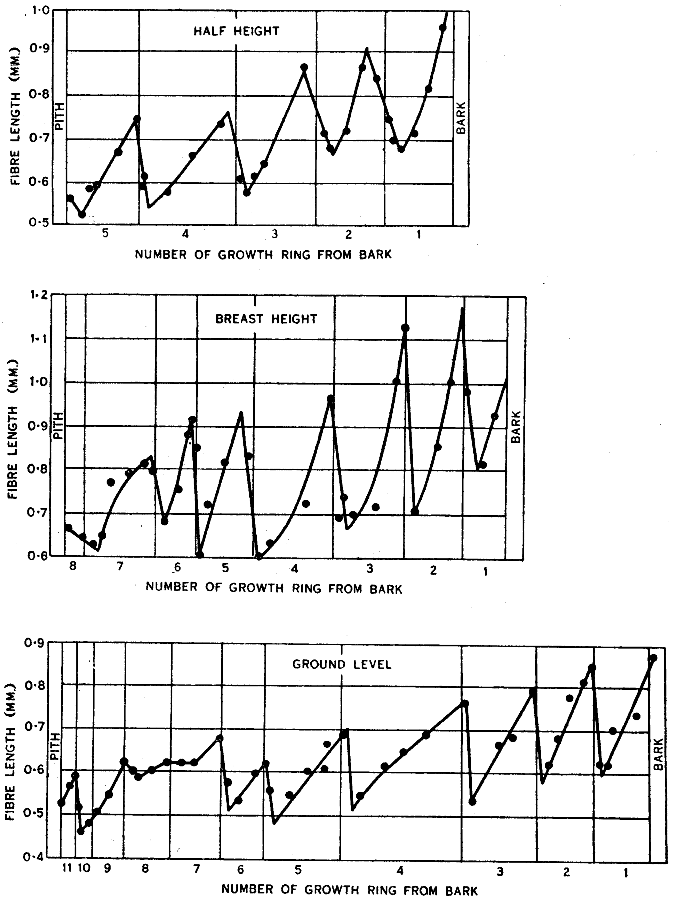

Fig. 4.—Variation of fibre length with position in growth ring, height in tree, and number of growth ring from the bark in *Eucalyptus gigantea.*

for a few weeks until the resurgence of cambial activity, the growth rate has reached a very low level. This period may therefore be considered as constituting a dormant period. The absence of the first band of abnormal tissue from the ground level specimens in the 1944-45 ring is confirmatory evidence of at least a short period of dormancy between the last-formed late wood and the resurgence of growth and this period may extend well into the spring at the lower levels in the stem.

(*f*) *Fibre Dimensions and Growth Rate*

(i) *Variation in Fibre Length*.—The results of fibre length variation at three levels within the one tree are presented graphically in Figure 4. In nearly all growth rings irrespective of height there is an increase in fibre length from early wood to late wood followed by a sudden drop in passing to the early wood of the next ring. This observation has been extended to other angiosperm woods, and has been found to be a principle generally applicable to woods with distinct growth rings (Bisset, Dadswell, and Amos 1950). Some

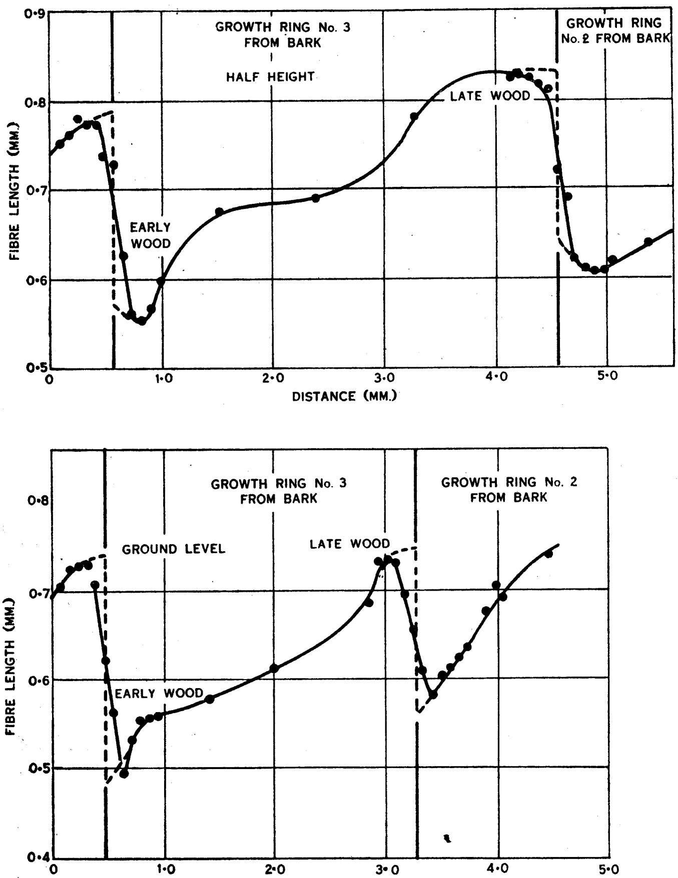

Fig. 5.—Variation of fibre length within a single growth ring of *Eucalyptus gigantea* at half height and ground level.

irregularities were apparent near the pith at ground level but in the outer rings, where positioning and general technique were of a high degree of accuracy, the phenomenon is most striking.

The 1942-43 growth ring was selected for more detailed study. Results of fibre length measurements at various positions in this ring, both at ground level and half height, are shown in Figure 5. It is fairly obvious that there is, in fact, a very sudden drop in length from the last-formed late wood of one growth ring to the first-formed early wood of the next. Although in Figure 5 results of fibre measurements in the region of the junction between late wood and early wood indicate a gradual drop it is a matter of simple mathematics

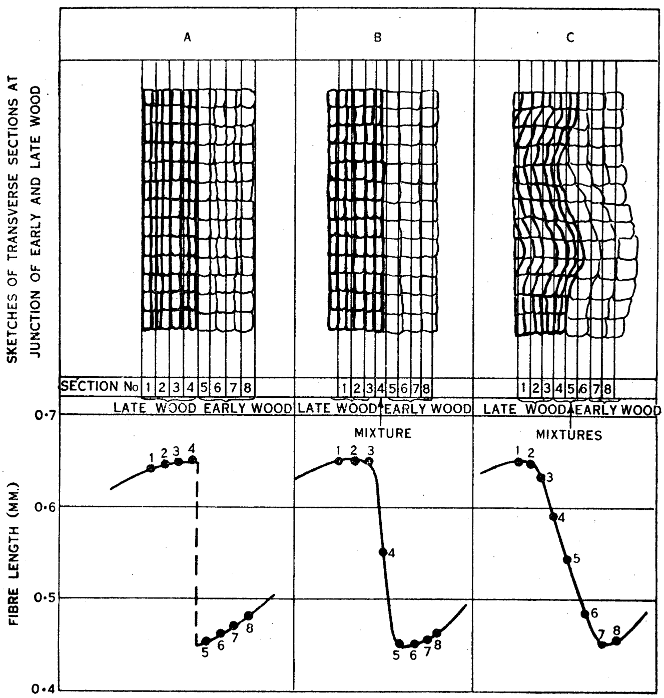

Fig. 6.—Effect of curvature of late wood-early wood junction on the shape of the fibre length distribution curve.

(A) Straight early wood-late wood junction. Tangential longitudinal late wood sections completely distinct from early wood sections, giving rise to "discontinuity" in fibre length distribution curve.

(B) Straight early wood-late wood junction but section No. 4 contains both early and late wood fibres; hence intermediate value on sloping fibre length curve.

(C) Irregular (common) early wood-late wood junction causing several sections to contain varying proportions of late and early wood fibres and giving rise to an apparent gradual decrease in fibre length from late wood to early wood.

to demonstrate that the actual results obtained and plotted are due partly to the fact that the junction between late wood and early wood is never a straight line and partly to the thickness of the sections employed for maceration. This is shown in Figure 6 which is self-explanatory.

The results obtained for the 1942-43 growth ring have, in Figure 7, been plotted against time during the growing season, the position-time transposition being obtained from Figure 1. This transposition is important for correlation of fibre lengths with growth rate and for such a comparison the growth rate curves have been added to Figure 7. It is immediately apparent that at the period of maximum growth rate the shortest fibres are developed and conversely that at the period of minimum growth rate the longest fibres are formed. This opposed relationship is particularly striking at ground level. At half height

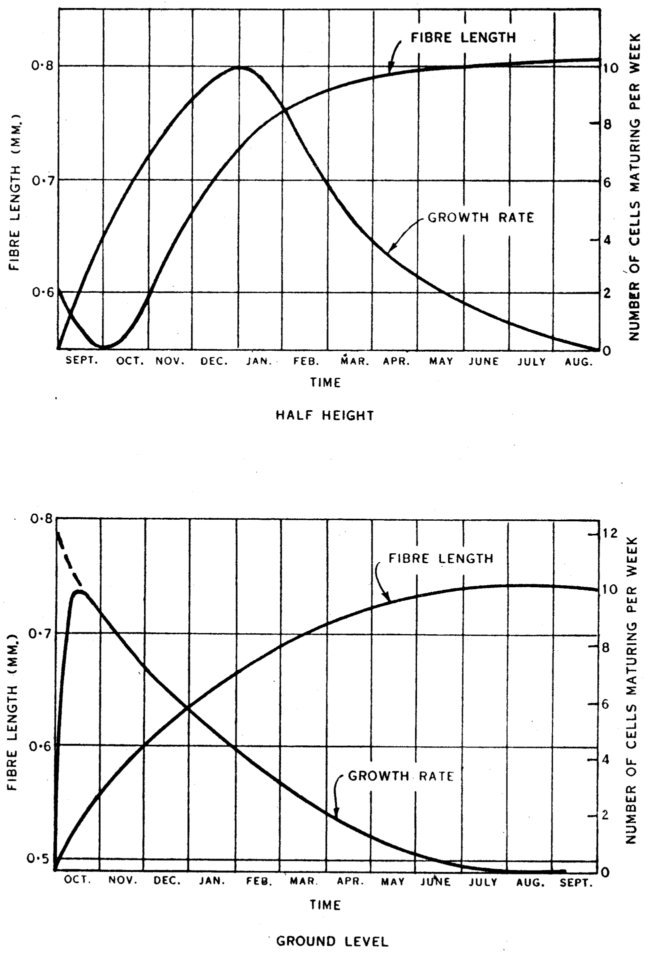

Fig. 7.—Comparison of growth rate and fibre length. (Fibre length data from Figure 5 with abscissae adjusted so that equal intervals represent equal time intervals.)

the same general features are observed although the positions of maximum growth rate and minimum fibre length are not nearly so coincident. Variation of this type can be expected where average data are compared with individual observations.

The accommodation of fibres of varying length within the one growth ring can be accounted for to some extent by the variation in fibre overlap from early wood to late wood. Actual observation has shown that the degree of overlap can be measured and it was found that the amount of fibre involved in such overlap was approximately twice as great in late wood as in early wood fibres. Fibres from first-formed early wood and last-formed late wood of the one growth ring are depicted in Plate 3, Figures 3 and 4.

(ii) *Variation in Fibre Diameter*.—Results of measurements of the radial diameters of fibres through the 1942-43 growth ring at three levels in the one tree are shown graphically in Figure 8. During the later part of the growth period the radial diameters progressively decrease, reaching a minimum in the late wood. Resurgence of growth after the dormant period is accompanied by a sudden increase in radial diameter. The curves for fibre diameter variation at the three levels show a striking similarity to the growth rate curves (see Figure 2*C*) and it is apparent that where growth is rapid fibre diameter is at a maximum and where growth is slow fibre diameter is at a minimum. It is also apparent that the shortest fibres have the greatest diameter and the longest fibres the smallest diameter.

At half height the fibres do not reach their maximum radial diameter until some time after the commencement of new growth in the spring, whereas at ground level maximum diameter coincides with resurgence of cambial activity. This agrees with the observed variation in growth rate. In photomicrographs of the 1942-43 growth ring taken at ground level and half height (Plate 3, Figs. 1 and 2) it is evident that at ground level, the first-formed fibres have the largest radial diameters, but at half height the first-formed fibres are somewhat thicker-walled and smaller than those formed subsequently.

(iii) *General*.—The results reported provide a further example of the principle so ably expounded by Thompson (1942), namely that growth and form are intimately connected and that one can frequently be deduced if the other is known. In the present case it appears that the growing conditions greatly influence the structure of the organism and it is of interest to note the magnitude of the variation in fibre dimensions, one of which, the radial diameter, changes with the growth rate, and the other, the length, changes in opposition to it. The variations have been summarized in Figure 9 in which a photomicrograph of the same growth ring has been included for comparison. From this figure it is apparent that, if the minimum length of the fibres within a ring be designated by L, the maximum length is approximately $3L/2$; from Figures 1 and 2 it is also apparent that, if the minimum radial diameter be designated by r, the maximum is approximately $9r/4 = (3/2)^2r$. Since the tangential diameter of the fibres is nearly constant the indication is that, within a particular growth cycle, the volumes of the maturing elements vary inversely as their lengths, i.e. directly as the growth rate.

The outcome of the study of fibre dimension in this species has been to elucidate a principle of growth in woody angiosperms which appears to be of general application, and to complete a pattern of growth investigated many years ago by Sanio (1872) who found that average fibre lengths in successive growth rings showed an initial increase, the increase decreasing in an exponential manner from year to year. Superimposed upon this overall variation is an

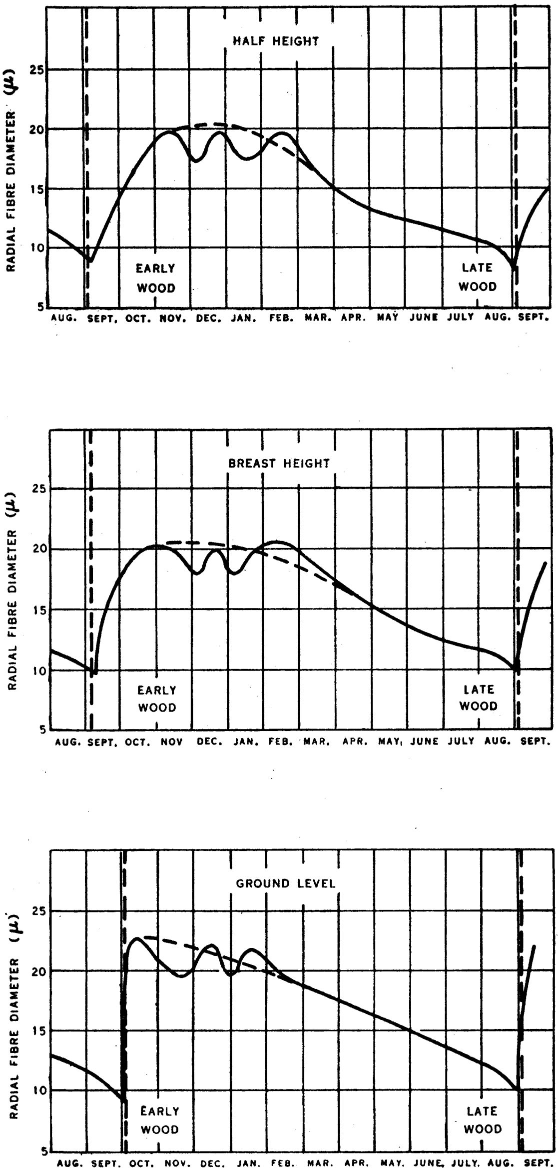

Fig. 8.—Variation in fibre diameter within the same growth ring at various levels in the tree. The curves shown - - - smooth over small variations during the growth period that have no general significance.

annual variation which is intimately connected with the variation in growth rate during the seasonal growing periods.

(g) *Anomalous Tissue*

As previously mentioned, the two bands of anomalous tissue occurring at half height in all trees from the area are characteristic for the 1944-45 growth ring and serve as an identification feature for the ring. Microscopic examination of the tissue revealed that the fibrous cells produced were tangentially expanded and that the ray cells had proliferated and were frequently divided by vertical walls parallel to the direction of the ray. Large numbers of more or less isodiametric cells were produced, as illustrated in Plate 2. Vessels between the two bands were completely tylosed and without function.

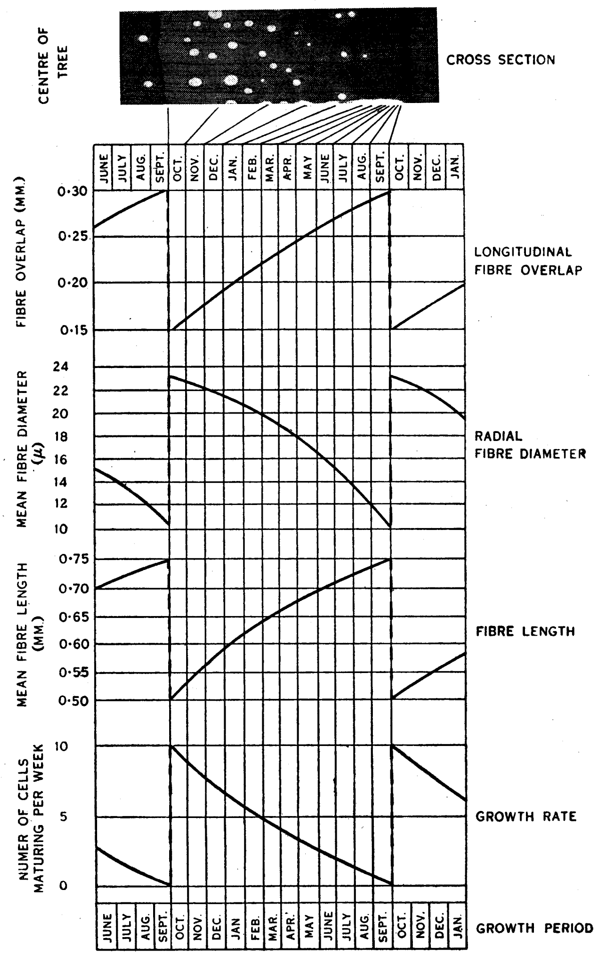

Fig. 9.—Idealized correlations of growth rate and fibre dimensions at ground level in *Eucalyptus gigantea*.

In an effort to determine the reasons for the formation of this tissue climatic data for the area were obtained. These data have been summarized in Table 5, from which it will be apparent that, at the time the tissues were formed, namely early in the 1944-45 growing season, the saturation deficit and temperature were higher than normal and the rainfall lower. Furthermore, these conditions followed a long, dry winter and were more severe than had been experienced in the previous six years for which data were available. The temperatures, although high for this period of the year, were not as high as summer temperatures. It is, however, probable that the lack of available moisture after the dry winter and the unusually high saturation deficit were responsible for overtaxing the water balance within the trees at a time when the young shoots were developing. It would therefore appear that the tissues were laid down under conditions corresponding to drought when the trees were relatively poorly equipped to resist a severe climate. The general occurrence of the two bands of this tissue in the young trees of *E. gigantea* from the area specified is a valuable reference point for any further study of trees from the same area.

TABLE 5

CLIMATIC DATA LATE AUGUST TO MID OCTOBER

Summary for Years 1939-1944

Period	Saturation Deficit (in. Hg) 1944	Saturation Deficit (in. Hg) Average 1939-1943	Rainfall (points) 1944	Rainfall (points) Average 1939-1943	Temperature (Max.) (°F.) 1944	Temperature (Max.) (°F.) Average 1939-1943
26.viii.–2.ix.	0.33*	0.20	2	52	65*	62
2.ix.–9.ix.	0.42*	0.24	0†	58	70	68
9.ix.–16.ix.	0.24	0.25	15	62	65	69
16.ix.–23.ix.	0.43*	0.25	0†	90	72	70
23.ix.–30.ix.	0.42*	0.29	30	25	78*	72
30.ix.–7.x.	0.41	0.34	9	61	78*	76
7.x.–14.x.	0.82*	0.33	0†	89	87*	71
14.x.–21.x.	0.51*	0.38	—	—	88*	76
Mean	0.45	0.26	8	62	75	68

* Highest value recorded for the period in any year.
† Lowest value recorded for the period in any year.

V. CONCLUSIONS

(i) Growth of *Eucalyptus gigantea* Hook. f. in the Australian Capital Territory continues well into the winter months, definite late wood formation beginning as late as the end of May.

(ii) There was a comparatively short period of dormancy at the end of the growing period and before the recommencement of growth in the early spring (beginning of September) in the Australian Capital Territory trees examined.

(iii) Resurgence of growth began in all trees at the higher levels and was not observed at ground level until 3-4 weeks after its inception at half height.

(iv) The growth rates varied at different levels; the maximum growth rate for the period under observation was reached at ground level just a few days after inception of growth for the season although at half height the maximum was not reached until several months had passed.

(v) The comparative absence of vessels from the first-formed early wood is a feature of the mainland trees of this species; in the specimens examined it was a particularly noticeable feature of the outer rings at ground level, but less obvious at higher levels and in rings close to the centre of the tree.

(vi) It has been suggested that this characteristic feature of late production of vessels after commencement of growth is related to distance from the crown and a possible mechanism has been discussed.

(vii) The Tasmanian specimens examined did not show either distinct growth rings or a vessel-free zone in the first-formed early wood; this difference from the majority of mainland specimens has been ascribed tentatively to variations in climate and environment rather than to any varietal difference.

(viii) It was continually found that the fibres of the early wood were shorter than those of the late wood and that there was a sudden decrease in fibre length from the late wood of one growth ring to the first-formed early wood of the next; on the other hand, the early wood fibres were found to have a consistently larger radial diameter than the late wood fibres. Thus there was a definite correlation between growth rate and fibre dimensions, the shortest, widest fibres of any one growth ring were laid down at the period of maximum growth rate and conversely the longest, narrowest fibres were laid down at the period of minimum growth rate. It has been shown that the greater length of the late wood fibres is accommodated by the greater amount of fibre overlap.

(ix) A relationship has been observed between the formation of certain anomalous tissue during the early portion of the 1944-45 growing period and climatic conditions at the time; it has been suggested that this particular tissue was formed in response to severe drought conditions.

VI: Acknowledgments

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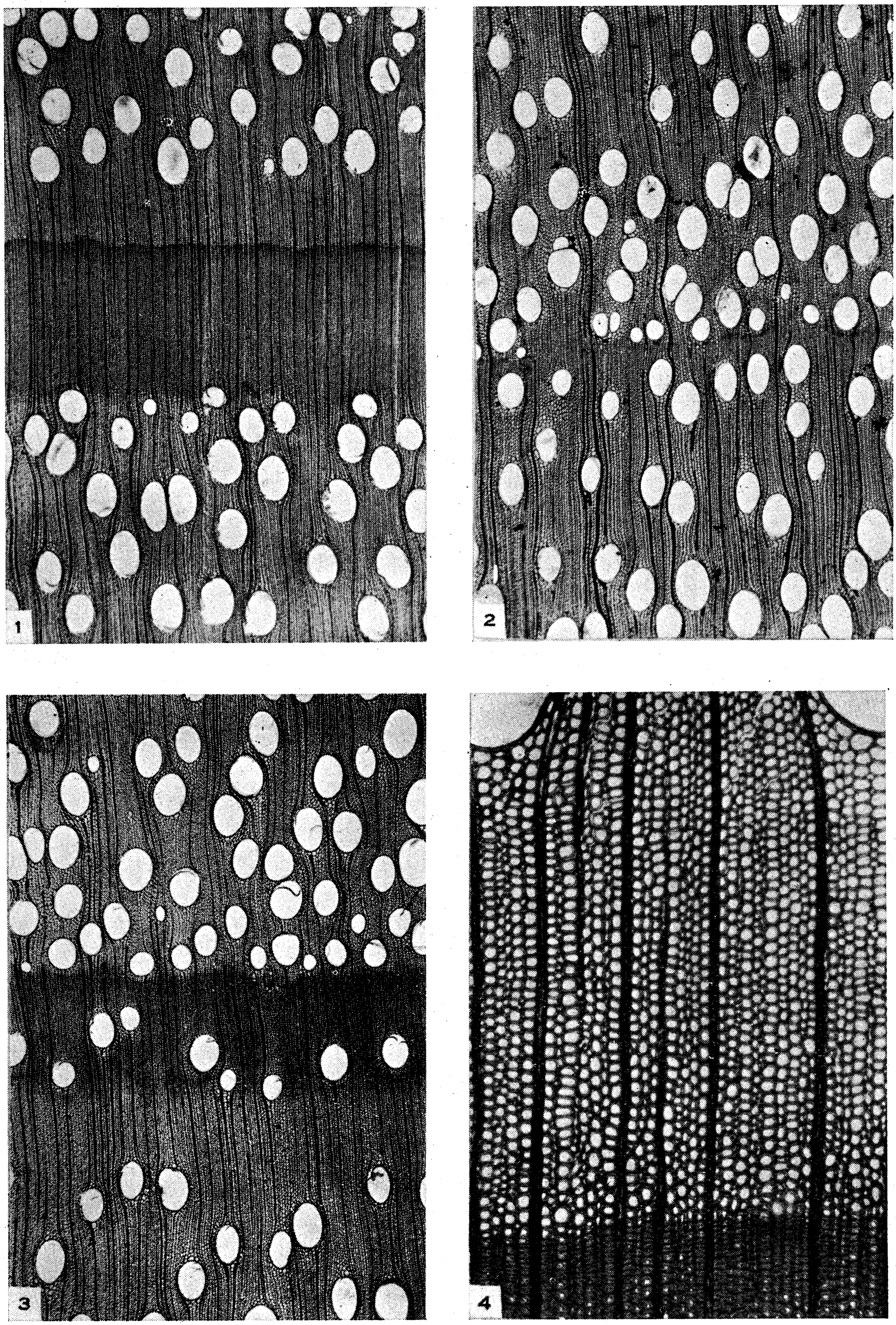
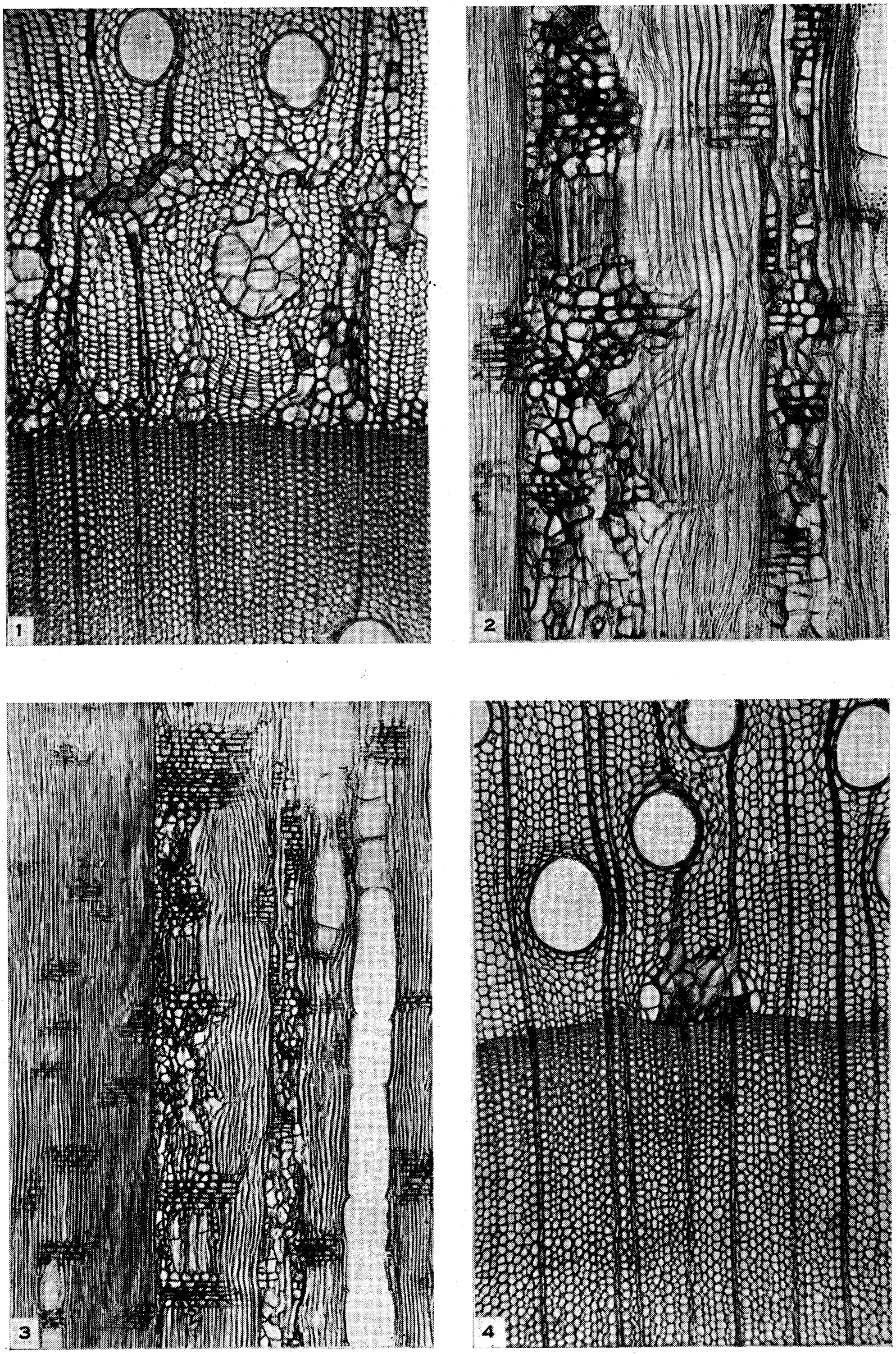


Amos, Bisset, and Dadswell.—Wood Structure in Relation to Growth in *Eucalyptus gigantea* Hook. f.



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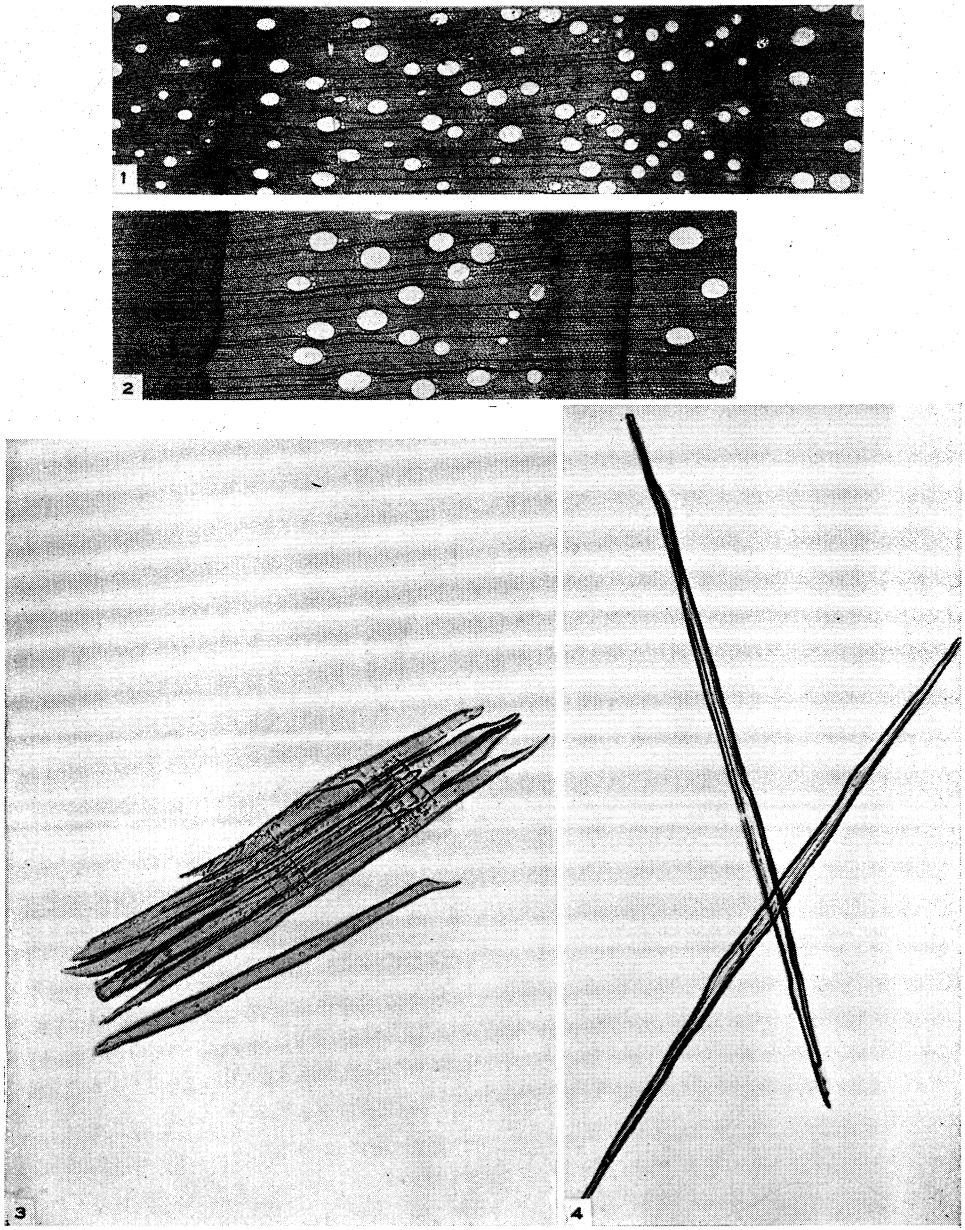

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EXPLANATION OF PLATES 1-3

PLATE 1

Fig. 1.—*Eucalyptus gigantea,* grown in Australian Capital Territory, showing band of late wood and early wood without vessels. x 25.

Fig. 2.—*E. gigantea,* grown in Tasmania, showing narrow and indistinct late wood with vessels formed early in the early wood. x 25.

Fig. 3.—*E. gigantea,* intermediate type, sometimes found in mainland specimens, showing distinct band of late wood well supplied with vessels, and a new crop of small vessels formed in the early wood. The vessels become larger in the later early wood. x 25.

Fig. 4.—*E. gigantea,* grown in Victoria, showing the band of early wood without vessels and distinct growth check at the end of late wood formation. x 120.

PLATE 2

Fig. 1.—Transverse section of *E. gigantea,* half height, grown in the Australian Capital Territory, showing two bands of abnormal tissue at the commencement of the 1944-45 growth ring and about 25 cells later. Vessels tylosed between the bands. x 100.

Fig. 2.—Longitudinal radial section of *E. gigantea,* half height, grown in Australian Capital Territory, showing two bands of abnormal tissue. x 100.

Fig. 3.—As for Figure 2, showing two bands of abnormal tissue, with normal vessel and fibres developed further out. x 50.

Fig. 4.—Transverse section of same tree at ground level showing small amount of abnormal tissue corresponding to the second band in Figure 1. x 100.

PLATE 3

Figs. 1 and 2.—The different *initial* rates of growth in the third annual growth ring from the bark in a tree of *Eucalyptus gigantea* at half height and ground level are shown by the smaller radial diameter of the fibres and their darker appearance at half height (Fig. 1) compared with the more open texture of the ring at ground level (Fig. 2). There is also a larger number of vessels and fibres at half height. The number of fibres formed before vessels are formed is markedly different at the two levels.

Fig. 3.—Early wood fibres.

Fig. 4.—Late wood fibres of the same growth ring as Figure 3. The photomicrographs show the short, stubby nature of early wood fibres and the long, tapering character of late wood fibres. The extent of overlap is indicated by the rather abrupt shoulders near the end of the early wood fibres. In the late wood fibres these shoulders are much further from the ends and are more sloping.